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Distribution, development and functioning of mycelial cord systems of decomposer basidiomycetes of the deciduous woodland floor

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On the floor of the majority of deciduous woodlands, especially those where logs, branches, stumps and leaf litter are abundant, networks of mycelium in the form of discrete, filamentous aggregations can usually be found (Fig. 1). These may spread for many metres through the litter and upper soil horizons and are often highly branched with many cross links. In the past such aggregations have been termed 'strands' or 'syrrotia' (De Bary, 1887; Falck, 1912; see also Jennings: Chapter 7; Watkinson: Chapter 8; Read: Chapter 10) but, as the former term can be interpreted literally as single hyphae, the term 'mycelial cords' is preferred here.

Production of cords is due to a change from divergent to coherent growth (Gregory: Chapter 1, Mode 7) and as such their constituent hyphae show a degree of co-ordination greater than that which exists between the individual hyphae of a vegetative colony. They are produced by a wide variety of fungi from a range of habitats but are generally best developed in the Basidiomycotina. As will become evident, considerable variation exists regarding the dimensions attained by wood- and litter-inhabiting Basidiomycotina.

Mycelial cords are superficially similar to rhizomorphs such as those produced by *Armillaria* species. Both are aggregations of hyphae which undergo differentiation to varying degrees, but they differ in that rhizomorphs are fully autonomous and grow apically whilst cords are built up more gradually around a mycelial framework. However, intermediate forms between cords and rhizomorphs do exist as in *Phallus impudicus* (Butler, 1966).

As mentioned by Gregory (Chapter 1) it is still not clear what promotes cord initiation and growth under natural conditions, although various stimuli have been shown to elicit initiation in culture (Table 1). Watkinson (1975; see also Chapter 8) has proposed that for *Serpula lacrimans* leakage of nitrogenous nutrients from leading hyphae plays a

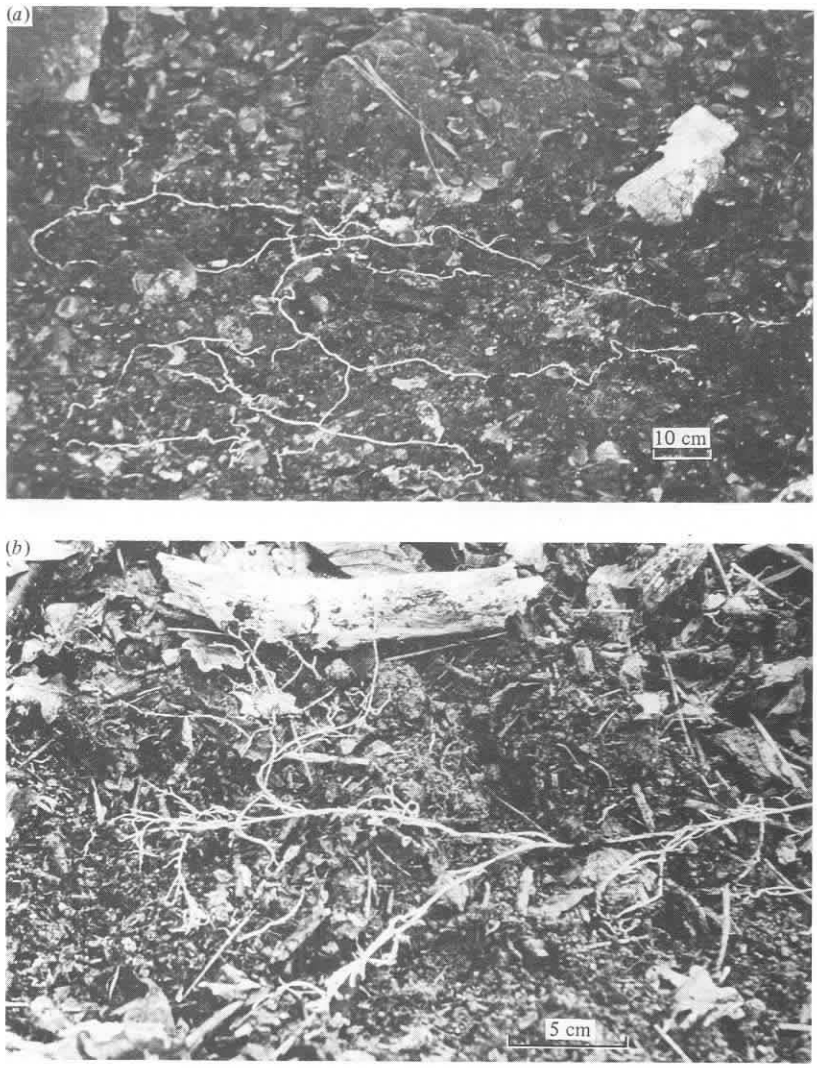

Fig. 1. (a) Excavated cord system of *Phanerochaete laevis* (Thompson & Rayner, 1982*a*). (b) Detail of the periphery of a system of *Phanerochaete velutina*.

Table 1. *Stimuli which elicit the initiation of mycelial cords and rhizomorphs*

Species tested	Stimulus	Source
Agaricus bisporus	Fresh soil placed on compost colonised by this species (in soil tubes)	Garrett, 1954
A. bisporus	Very low nutrient concentrations in the surrounding media	Mathew, 1961
Agaricus campestris	High moisture conditions	Hein, 1930; Styer, 1930
Calvatia sculpta	The presence of a permeable physical barrier (e.g. cellophane) between the mycelium and a medium which would not otherwise support the formation of cords e.g. 2% malt agar or cornmeal agar	Bellotti & Couse, 1980
Coniophora cerebella	Neutral part of the ethyl ether extract of heat-treated pine wood	Glasare, 1970
Helicobasidium purpureum	Translocation in leading hyphae	Valder, 1958
Phymatotrichum omnivoroum	Inocula placed on slides in a sterile, moist chamber	Rogers & Watkins, 1938
Poria xantha	Cu^{2+}	Hirt, 1949
Serpula lacrimans	High C : N ratio; $NaNO_3$	Watkinson, 1975
S. lacrimans	Translocation in leading hyphae	Watkinson, 1971
Xylaria polymorpha	Transfer to cultures of 'producer' fungi, e.g. *Pythium mamillatum*, *Fusarium oxysporum*, *Fusarium caeruleum* and *X. polymorpha*	Park, 1963
Armillaria mellea	Certain amino acids	Weinhold & Garraway, 1966
A. mellea	Sufficient nutrition; critical C : N ratio	Garrett, 1953
A. mellea	Ethanol	Weinhold, 1963; Sortkjaer & Allermann, 1972
A. mellea	Indole acetic acid and compounds related to the shikimic acid pathway; amino benzoic acid	Garraway, 1970

Table 1. (*cont.*)

Species tested	Stimulus	Source
A. mellea	Acetate	Sortkjaer & Allermann, 1972
A. mellea	Figwood extract	Weinhold, Hendrix & Raabe, 1962
A. mellea	Moist conditions	Townsend, 1954
A. mellea	Oils and fatty acids	Moody, Garraway & Weinhold, 1968
A. mellea	*Aureobasidium pullulans*	Pentland, 1965
Sphaerostilbe repens	Diffusion of a factor (soluble in water, non-volatile, stable at laboratory temperature and inactive at 100 °C) produced by *Penicillium* spp., *Aspergillus* spp. and *Verticillium* spp. in culture medium	Botton & El-khouri, 1978
S. repens	Continuous presence of calcium in the culture medium	Botton, 1978

part. When the hyphae in a growing colony have taken up nutrients from the culture medium so that most of the nutrient material is in the mycelium, the first-formed hyphae are thought to become more permeable with age, and formation of cords results from further growth around these. However, cord formation resulting from intertwining of undifferentiated hyphae can also occur during outgrowth of *S. lacrimans* into non-sterile sand (A. D. M. Rayner, personal communication).

At least five advantages of mycelial aggregation into cords can be envisaged: protection against deleterious external agencies; channelling of resources (nutrients and water), allowing outgrowth from suitable bases into an environment in which these are deficient; nitrogen conservation; enhancement of inoculum potential; and amplification of the sensitivity of individual hyphae to external stimuli, enabling directed growth responses (see also Jennings: Chapter 7; Watkinson: Chapter 8; Read: Chapter 10; Rayner *et al.*: Chapter 23).

With regard to protection, the buffering effect of aggregation of hyphae into cords may endow a fungus with greater resistance to environmental fluctuations and extremes than could otherwise be

contended with by isolated hyphae. Additionally, cords may serve as a means of protection against other organisms, including anti-mycotic-producing bacteria, parasitic or other fungi and grazing microfauna. This protective function may be enhanced by production of calcium oxalate, which, as discussed by Jennings (Chapter 7) may be a characteristic feature of certain actively-translocating systems. Mycelia of terrestrial fungi can contain high calcium concentrations (Stark, 1972; Todd, Cromack & Stormer, 1973; Cromack *et al.*, 1977) and the outermost hyphae of cords of *Phanerochaete velutina, Phanerochaete laevis, Phallus impudicus* and *Tricholomopsis platyphylla* are characteristically heavily encrusted with calcium oxalate (Thompson, 1982). The reduction of pH in the immediate vicinity of cords which is a consequence of calcium oxalate production will tend to suppress bacteria which are generally relatively intolerant of low pH (Gray & Williams, 1971), and might also underly lysis and replacement of other mycelia in combative interactions (cf. Rayner & Webber: Chapter 18).

As has already been indicated by Jennings (Chapter 7) and Watkinson (Chapter 8) aggregation of individual hyphae into cords may allow resources to be channelled so that direct and economical movement of nutrients and water may occur between a colonised 'food base' and the advancing edge of a system and/or vice versa. It seems likely that translocation occurs within mycelial cords as they often extend for many metres between food bases and represent the only connection between the growing mycelial margin and either fruit bodies or food bases. Also they contain elements of wide diameter ('vessel' hyphae, Fig. 2), which from anatomical considerations seem likely to have low resistance to solution flow. These can be very large, up to 60 μm in diameter in *Phanerochaete velutina* for example. There is now very substantial evidence from laboratory studies that cords of *S. lacrimans* translocate water and nutrients (Butler, 1958; Weigl & Zeigler, 1960; Watkinson, 1971; Clarke, Jennings & Coggins, 1980; Hornung & Jennings, 1981; Brownlee & Jennings, 1982; Thompson & Jennings, unpublished). Estimates of the velocities of various radioactive isotopes through mycelia of *S. lacrimans* are all of the order of 25 cm h^{-1} (Jennings: Chapter 7).

The role which cords may have in nitrogen conservation has already been discussed by Watkinson (Chapter 8). Briefly, by growing as aggregated structures, fungi can re-utilise via autolysis the nitrogenous products of old hyphae. Further, pure culture studies indicate that development of cords of *S. lacrimans* depends on high C:N ratios.

Buffering against adverse external factors, channelling and efficient utilisation of resources contribute to another important feature, enhancement of the invasive force, or inoculum potential (see also Rayner *et al.*: Chapter 23). By the same token, in circumstances where suitable substrata are discontinuously distributed, efficiency is gained if wastage of biomass by growth in the wrong direction can be minimised. Whereas individual hyphae may be relatively incapable of long-range responses to suitable external stimuli, their individual responsiveness may be amplified many times by aggregation into cords, promoting directed growth. Evidence that such directed growth may play a role in colonisation processes and mycelial interactions will be given below.

Despite these potential advantages many fungi are, of course, successful without producing cords. Amongst wood decomposers these include *Coriolus versicolor* and *Phlebia merismoides* which colonise via air-borne spores (Carruthers & Rayner, 1979). Although cord formation is not therefore a pre-requisite for success the probability is that it represents an important adaptation whereby, in suitable habitats, colonisation of substrata may be effected from pre-existing vegetative mycelia. Nonetheless, with the exception of the work on *S. lacrimans* and recent studies of sheathing mycorrhizas (Read: Chapter 10), this probability and its consequences have attracted surprisingly little attention. The aim of this chapter is to examine these issues, and their

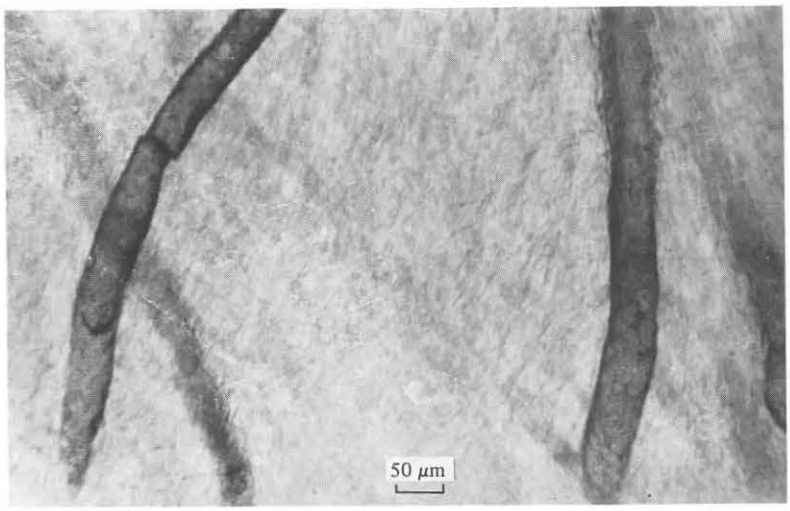

Fig. 2. Micrograph of a mature cord of *P. laevis* showing vessel hyphae (Thompson & Rayner, 1982*a*).

importance for understanding mycelial biology of that somewhat neglected group of fungi mentioned at the outset, which inhabit the deciduous woodland floor as more or less extensive mycelial systems and bring about decomposition of accumulations of woody and other litter.

Distribution

Observations from direct field sampling and excavations

Considerable variation occurs in the form of the mycelium of decomposer basidiomycetes inhabiting the woodland floor, the extent of aggregation ranging from short, woolly mycelial tufts originating from the bases of basidiocarps, as with *Clitocybe flaccida*, to well-defined individual cords up to 5 mm in diameter, which often extend several metres from the associated basidiocarps and also occur freely in the absence of the latter, as with *Phanerochaete velutina*. There seems to be a correlation between mycelial form and ecological role in that it is those fungi which invade wood which form the more clearly-defined cord systems. Although some of these fungi, such as *P. velutina*, *Phallus impudicus* and *Tricholomopsis platyphylla*, can also decompose leaf litter, this activity is usually marked only in the immediate vicinity of bulky, woody substrata. By contrast, those fungi which specifically rot litter usually form diffuse systems with ill-defined fragile cords or loose aggregations of mycelium. *Mutinus caninus* is intermediate, forming defined cords associated with woody litter components, and more diffuse mycelium in leaf litter or sawdust. This difference in form between the mycelium of litter decomposers and wood decayers may be linked to the nature of the resources they attack. Substrata exploited by litter decomposers are widespread and diffuse and require a correspondingly diffuse, spreading system for exploitation. Wood-decaying fungi on the other hand exploit larger, bulkier resources which are often spatially separated and these fungi produce bulkier and more extensive systems of cords along which translocation must occur. As discussed earlier, these fungi are effectively concentrating their inoculum potential and thereby their invasive force.

Field excavations made by careful removal of soil and litter away from cord systems of wood-decaying species reveal that in all cases such systems are composed of networks of cord, which are generally relatively thick and sparsely branched in older regions and thinner and extensively branched peripherally (Thompson & Rayner, 1983) (Fig. 1). The cords of *P. velutina*, for example, often measure up to 4 mm in

diameter in older regions and up to 1.5 mm in younger peripheral parts. The most extensive systems found in terms of total length were those of *Phanerochaete velutina* (up to 31.7 m), *Phallus impudicus* (up to 24.8 m), and *Steccherinum fimbriatum* (22.6 m); systems of other species such as *Tricholomopsis platyphylla* and *Phanerochaete laevis* were usually 15 m or more in total length. Grainger (1962) also found the cord systems of *Phallus impudicus* to be fairly extensive – of the two systems he excavated the longest was over 16 m in overall length. *P. velutina, P. impudicus* and *T. platyphylla* are common and widespread in British woodlands and as less-common species and other unidentified fungi also form substantial cord systems it is likely that cord-forming fungi as a group are very important in terms of the amount of living fungal biomass present in the soil and litter of our forests. The dimensions and overall extent of cord systems such as those referred to above would seem to suggest that they have persisted, in some cases for considerable periods of time. It is therefore reasonable to suppose that they may be relatively resistant to various external agencies as discussed earlier.

The ubiquity of cord-forming fungi on the woodland floor is further demonstrated by the extent to which they are present in arrays of suitable substrata. For example, in a study of decomposition of suppressed oak trees in two even-aged plantations at Savernake Forest, Wiltshire, and the Forest of Dean, Gloucestershire (Fig. 3), colonisation of the tree bases was studied by three methods: direct observation of mycelial systems and fruit bodies on the bases; direct incubation of wood slices from the bases in polythene bags; and isolation into pure culture from small wood chips taken from each different decay region (Thompson & Boddy, 1983). Cord-forming fungi and two *Armillaria* species (*A. bulbosa* and *A. ostoyae*) were found to be the most important in terms of frequency and volumes of wood occupied, and were present during all stages of decay. *Phanerochaete velutina* and *Phallus impudicus* were the most important cord-forming species, being found in 26 to 37.5% of sampled trees at these two sites (Table 2). It is interesting to note, however, that at an older oak stand (planted 1929) in the Forest of Dean, observations of fifteen suppressed oak trees indicated that the roots of eight were colonised extensively, and almost exclusively by *Tricholomopsis platyphylla*, one by *P. velutina*, two by *A. bulbosa* and one by both *T. platyphylla* and *A. bulbosa*. Thus at this site *T. platyphylla* was the dominant cord-forming species. However, high frequencies of cords and fruit bodies of this fungus had been observed throughout the younger Forest of Dean site (planted 1943) where only

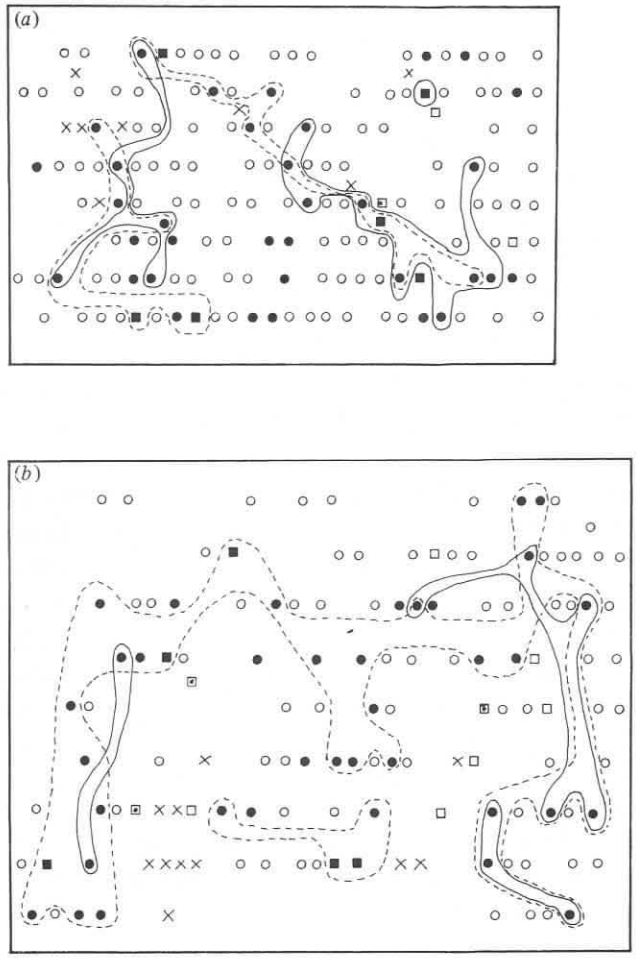

Fig. 3. Distribution of different mycelial types of *P. velutina*, *A. bulbosa* and *A. ostoyae* in (*a*) a 28 × 9 m site of p. 55 oak at Savernake Forest and (b) a 50 × 11 m site of p. 43 oak at Forest of Dean. Filled circle, sampled dead oaks; hollow circle, living oaks; filled square, sampled stumps of fallen suppressed oaks; hollow square, large oak stumps from trees grown previously on the site; X, trees other than oak; continuous line, delimitation of trees/stumps colonised by the same mycelial type of *P. velutina*; dotted line, delimitation of trees/stumps colonised by the same mycelial type of *A. ostoyae* at Savernake and *A. bulbosa* in the Forest of Dean. (Thompson & Boddy, 1983.)

Table 2. *Frequency of isolation of different fungi from roots of suppressed oak trees*

Fungus	Percentage of trees sampled	
	Savernake	Forest of Dean
Cristella sulphurea	2.5	2.3
Hypholoma fasciculare	7.5	11.9
Mutinus caninus	2.5	9.5
Phallus impudicus	30.0	33.0
Phanerochaete sp. 1	5.0	–
Phanerochaete sp. 2	–	16.6
Phanerochaete velutina	37.5	26.2
Tricholomopsis platyphylla	–	4.7
Unidentified sp.	2.5	14.2
Armillaria bulbosa	–	97.7
Armillaria ostoyae	72.5	–
Bjerkandera adusta	–	7.1
Collybia fusipes	7.5	7.1
Coriolus versicolor	2.5	–
Grifola frondosa	5.0	–
Phlebia merismoides	10.0	14.2
Stereum gausapatum	2.5	2.3
Stereum hirsutum	7.5	4.7
Other basidiomycetes	12.5	30.9
Ascocoryne sarcoides	15.0	2.3
Hypoxylon serpens	5.0	2.3
Xylaria hypoxylon	2.5	2.3
Other fungi	47.5	66.6

4.7% of sampled trees were actually colonised by it. Perhaps then this species occurs later than other cord-forming fungi in the tissues of suppressed oak trees or, alternatively, the older site may have been particularly 'good' for this species.

Considering colonisation of suppressed oak trees by cord-forming fungi and *Armillaria* species in particular (Table 3) it becomes clear just how important these fungi must be in the decay of such 'newly available' substrata. For example, 72.5% of sampled (suppressed) trees at Savernake forest were colonised by cord-forming species whilst the corresponding value for the Forest of Dean was 88%.

A further study which demonstrated the extensive distribution of cord-forming fungi in woodland habitats involved the colonisation, by cord formers, of freshly cut beech logs arranged experimentally on the floor of a mixed deciduous woodland (Thompson, 1982). This study

Table 3. *Percentage of roots of suppressed oak trees colonised by* Armillaria *species and cord-forming fungi*

Fungus	Savernake		Forest of Dean	
	Isolation and direct incubation	Field observations, isolation and direct incubation	Isolation and direct incubation	Field observations, isolation and direct incubation
Armillaria species[a]	42.5	72.5	88.0	97.7
Cord-forming fungi	55.0	72.5	69.0	88.0
Armillaria species and cord-forming fungi	27.5	52.5	69.0	88.0
Neither *Armillaria* species nor cord-forming fungi	30.0	7.5	12.0	2.3

[a] *A. bulbosa* at the Forest of Dean and *A. ostoyae* at Savernake.

indicated that colonisation occurred rapidly throughout the entire site. In fact within 33 months over 75% of all logs had become extensively colonised by cord-forming species, particularly by *P. velutina.*

Population structure

Although direct observations of the type just described provide an idea of the distribution of mycelial cord-forming fungi, for a more complete understanding, knowledge of the spatial distribution of individual genotypes in populations of these fungi is required. Since such information is limited, a detailed analysis of the spatial structure of a population of *T. platyphylla* has been made using the phenomenon of somatic incompatibility between secondary mycelia of this species (Thompson & Rayner, 1982*b*). When genetically and physiologically distinct mycelial types (individuals) are paired in culture they are mutually antagonistic (Rayner & Todd, 1979; Todd & Rayner, 1980), a reaction which provides a basis for the identification of individuals in the field and ultimately a key to the understanding of natural patterns of dispersal, establishment and vegetative spread of such fungi (Rayner & Todd, 1982; see also Frankland: Chapter 11; Rayner *et al.*: Chapter 23). Results from this study revealed that only a limited number of often extensive mycelial types were present throughout a site of 2.08 ha, i.e. of 113 isolates (from wood, cords and fruit bodies) only 22 different mycelial types existed (Fig. 4). In another study the population distributions of *P. velutina* throughout oak stands, containing suppressed individuals, at Savernake Forest and the Forest of Dean, were analysed. Using the technique described above to distinguish individuals, three different mycelial types of *P. velutina* were identified at Savernake and four at the Forest of Dean (Fig. 3).

This situation, where limited numbers of mycelial types of cord-forming species are distributed over very large areas of the forest floor, contrasts markedly with the situation which is found in airborne wood decay species such as *C. versicolor* and *Stereum hirsutum.* Here any one stump or branch may contain large numbers of antagonistic individuals separated by relatively undecayed interaction zones (Rayner & Todd, 1979). Distributions of the former type probably reflect the fact that *T. platyphylla* and *P. velutina* are capable of propagation via vegetative mycelial growth between food bases in the soil. The mycelium which spreads as cords between spatially-separated resources must be adapted to traverse the intervening regions between food bases which may often be hostile to fungal growth in nutritional, competitive and/or physi-

cochemical terms. Such an adaptation endows a single mycelial individual with the potential to occupy a very large territory.

It is important to realise that the pattern of arrival at and initial establishment in resources have important consequences. For example establishment from pre-existing mycelium, as well as being less susceptible than spores to adverse external influences, may be expected to lead to more rapid and extensive initial occupation of available space (i.e.

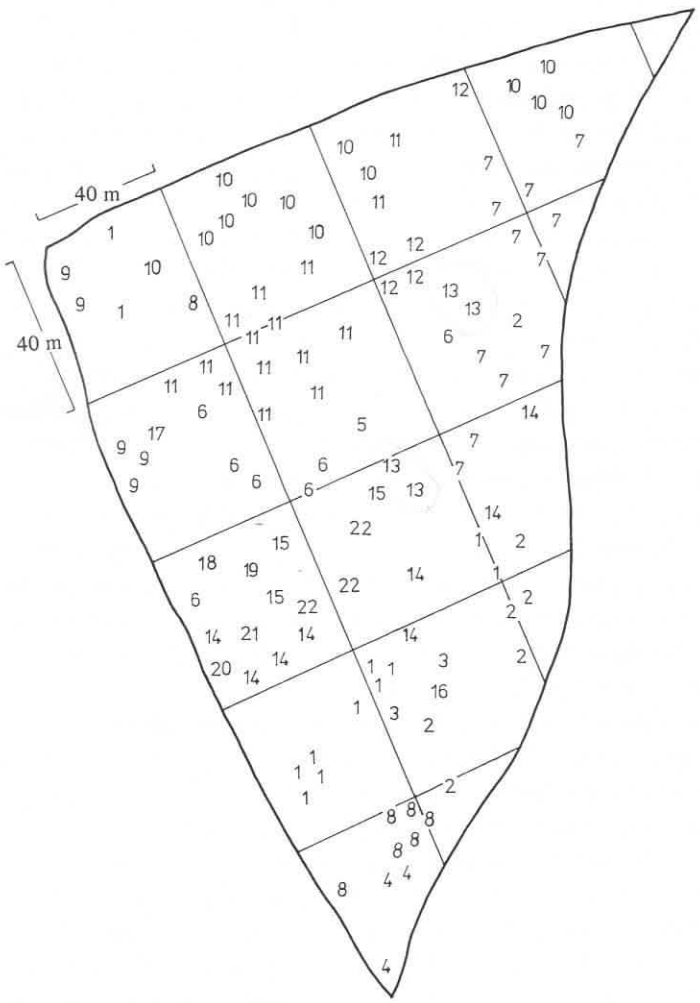

Fig. 4. Distribution of different mycelial types of *Tricholomopsis platyphylla*, indicated by different numbers. (Thompson & Rayner, 1982*b*.)

'resource capture') with consequently fewer individuals becoming established (Carruthers & Rayner, 1979; Rayner & Todd, 1979).

Considering the distribution of mycelial types of *T. platyphylla* (Fig. 4) and given that isolates of the same mycelial type originate from the same individual (as it is unlikely, in a heterogeneous population, that dikaryons sufficiently similar genetically to intermingle in culture should develop from separate colonisations from basidiospores), analysis of their distribution should provide insight into the dynamics of the mycelial population. Unfortunately only limited information was obtained regarding mating-type distribution in the population, due to poor viability of monospore isolates in culture (Thompson & Rayner, 1982*b*). Nevertheless we can, with informed speculation, suggest a variety of possible explanations to account for the observed population structure. Thus very extensive mycelial types (e.g. type 11, Fig. 4) may represent individuals which were established early on in the development of the population and have persisted until the present time; alternatively they may only be temporarily expansive (i.e. at the time of the study).

Individuals of more limited extent may represent remnants of formerly more extensive systems or initial stages in the development of systems which may, in time, become more extensive. As regards their origin it is possible that those neighbouring more extensive types may have arisen from the latter sexually from basidiospores, or, less probably, via somatic changes in parts of the mycelium. This is most likely when the neighbouring isolates concerned have interactional characteristics similar to those of the extensive mycelium. Thus, types 5, 6 and 12 (Fig. 4) may have arisen from type 11.

Different individuals in close proximity, however, may not necessarily always be related, as judged by their behaviour when paired in culture; e.g. types 1 and 3, although found comparatively close together were highly antagonistic. Equally, types 1 and 13, although weakly antagonistic and of similar interactional behaviour, were found over 60 m apart.

Certain mycelial types occupied defined areas from which other types were excluded (e.g. type 11, Fig. 4) whilst others had discontinuous distributions in that isolates of the same type were located considerable distances apart with the intervening space occupied by other types (e.g. type 1, Fig. 4). In the latter case, it may be that an originally continuous mycelium may break up and establish new centres, although the mechanisms underlying such break-up remain obscure.

It is difficult to be certain of the origin and development of mycelial

types occurring in peripheral regions of the site (e.g. type 9, Fig. 5). These types may be more extensive outside the limits of the sampling grid and may be in the process of invasion of, or elimination from, the sampling area.

Many of the questions raised above could, of course, be resolved by repeated surveys at the same site, and such consecutive samplings may be important in future population studies. One important factor which probably influenced the observed population structure of *T. platyphylla* is the occurrence of three past thinning operations at the site, the most recent being one year before sampling. These are likely to have had an effect via the sudden generation of new resources for colonisation, but this cannot be gauged with certainty without repeated samplings before and after thinning.

A number of studies, similar to the present, have been made for

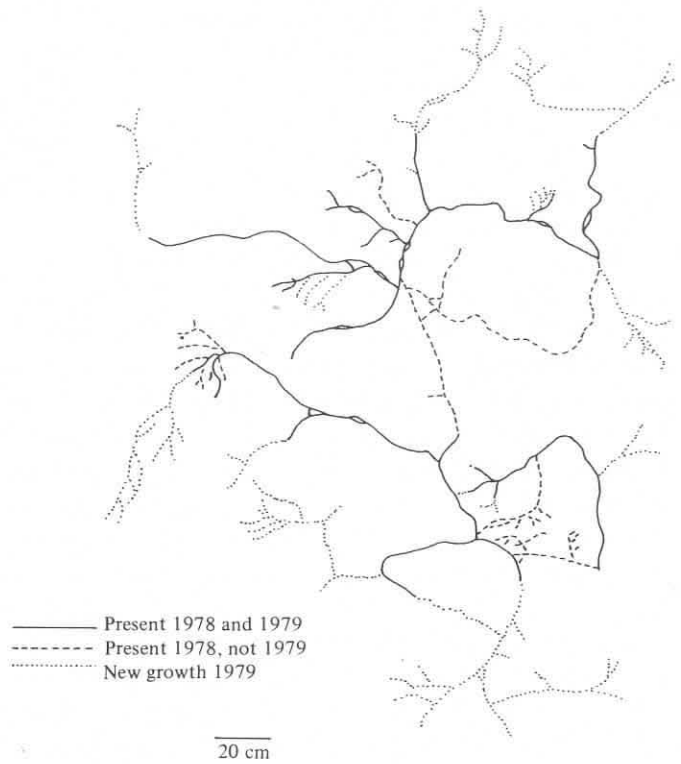

Fig. 5. Diagram illustrating development of a field system of *P. laevis* over a 13-month period. (Thompson & Rayner, 1982*a*.)

several important root-infecting forest pathogens including *Armillaria* spp. (Adams, 1974; Shaw & Roth, 1976; Rishbeth, 1978; Korhonen, 1978). *Phellinus weirii* Murr. (Childs, 1963) and *Phaeolus schweinitzii* (Fr.) Pat. (Barrett & Uscuplic, 1971). These have variously employed cultural characteristics, antagonism (though not always with a sound knowledge of the genetical basis for the reaction), and distribution of mating-type factors (which are not reliable indicators since isolates with the same factors may be derived from separate combinations of sib-related homokaryons) to identify mycelial types (often rather dubiously referred to as 'clones'). These have all served to indicate the different consequences of spread via vegetative mycelium and basidiospores. Thus, the rhizomorphic *Armillaria* species show similar distribution patterns (though normally with fewer types) to *T. platyphylla*, and in some instances isolates of the same type have been located as much as 450 m apart (Anderson, Ullrich, Roth & Filip, 1979). By contrast, different individual trees on the same site colonised by *P. schweinitzii* normally contain different genotypes of the fungus, and this is believed to be associated with basidiospore colonisation from the soil (Barrett & Uscuplic, 1971).

Development

In the field

Repeated excavation of systems of *P. impudicus, Phanerochaete laevis, P. velutina* and *T. platyphylla* in the field over periods of 12 to 14 months revealed how such systems may develop. New growth usually occurred at the periphery of each system but new cords could develop in central areas, often anastomosing with pre-existing cords. This more recent growth often developed after 'sprouting' had occurred following rainfall, and was substantial from some parts of systems but minimal from others. Little growth occurred during May to September. These observations suggest that moisture availability plays an all-important role in the dynamics of these systems. Those parts which died between successive examinations were often central or had previously been 'fans' of cords at the advancing edges of systems when they were first excavated (Fig. 5). Systems of *P. impudicus, T. platyphylla, Phanerochaete laevis* and *P. velutina* made 255, 260, 234 and 535 cm net new growth respectively, taking into account death within the systems. Development of the cord systems of each of these four species was very uneven with some parts growing at greater rates than others.

In the laboratory

In agar culture. Cord-forming fungi show variation in their readiness to produce cords in agar culture. Some species, e.g. *T. platyphylla*, show no signs of corded growth in these conditions; this may be due to the lack of a 'suitable' surface (i.e. one which can support corded growth). For example cord formation can be induced in *Calvatia sculpta* by the presence of a permeable physical barrier between the agar substratum and the growing mycelium (Bellotti & Couse, 1980). Other species, such as *P. velutina*, grow mycelially to the edge of the Petri dish when cords are formed which usually grow back over the mycelium towards the original inoculum. *P. impudicus*, however, produces cords more or less immediately after subculturing on agar media, with a very limited amount of mycelial growth occurring initially. This species resembles *Armillaria* species such as *A. mellea* and *A. bulbosa* which show limited mycelial growth but extensive rhizomorph formation.

Cord-forming species do not always grow uniformly on agar media. Sometimes, for example in colonies of *T. platyphylla*, regions of mycelium develop faster than the mycelium in the majority of the colony. Such changes resemble the phenomenon of point growth, observed in *S. lacrimans*, which occurs on media which produce relatively low growth rates (Coggins, Hornung, Jennings & Veltkamp, 1980). In this fungus point growth is thought to represent a response to environmental stress, although the mechanism of stimulation of growth at a particular part of the mycelium is not known.

In *Hypholoma fasciculare* colonies of two distinct morphological types are commonly found even when isolations are made from the tissue of a single fruit body (as described by Rayner, 1975). The underlying basis of this dimorphism is unclear and the phenomenon needs further investigation, particularly regarding the persistence and cord-forming capacity of each morphological type.

Cord initiation in cultures of *P. velutina, P. laevis* and *T. platyphylla* can be stimulated by beechwood volatiles (see also Table 1). In one instance cords up to 15 mm in length were induced by sterile beechwood shavings suspended 3 cm above growing mycelial colonies of *T. platyphylla* (Thompson, 1982). Such stimulation may be relevant to the phenomenon of directed growth towards potential resources suitable for colonisation.

In soil tubes. Autoclaved beech blocks ($\sim 2\,cm^3$) placed on to the surface of pure cultures of cord-forming fungi readily become permeated with

mycelium, and can then be used as inocula in laboratory studies of the outgrowth of cord-forming fungi from food bases into soil.

In one set of experiments six species were allowed to grow, in the dark, through tubes of non-sterile and sterile soil (Thompson & Rayner, 1982*a*, 1983). The patterns of development of cord systems of *P. velutina, P. impudicus, P. laevis* and *T. platyphylla* in tubes of unsterilised soil in the laboratory were similar to that occurring in the field. In all cases extension into the uncolonised soil occurred as much-branched and anastomosed systems of fine cords constituting 'fronts' of more or less constant width which were short-lived. These eventually lysed to become superseded by thick, relatively unbranched cords which were few in number but which maintained a connection between different parts of the expanding mycelium (Fig. 6). When the fungi were grown in sterile (γ-irradiated) soil, mycelial extension of *Steccherinum fimbriatum, Hypholoma fasciculare, P. impudicus, P. velutina* and *P. laevis* was reduced when compared with that occurring in non-sterile soil. *T. platyphylla* grew at similar rates in both sterile and non-sterile soils. Differentiation of the mycelium was affected by soil sterilisation in all the afore-mentioned species but to a lesser extent in *P. impudicus*. Those species which were affected developed luxuriant 'fan' mycelia which showed little differentiation into distinct cords (Fig. 6).

There are two possible explanations of this effect of soil sterilisation – changes in the structure, chemistry and nutrient status of the soil and the elimination of soil organisms. Gross changes in the physicochemical properties of the soil were probably not involved as γ-irradiation and autoclaving of soil gave similar results. However, both methods will result in the release of ammonia nitrogen (Salonius, Robinson & Chase, 1967) and other nutrients from previously-living organisms. As it has been suggested that cords form under conditions of low nutrient availability (Watkinson, 1971), so cord formation would not be expected to occur in sterile soil if this were the case. Alternatively, removal of soil micro-organisms, which may stimulate mycelial differentiation via production of morphogenetically-active substances, direct contact or competition for nutrients, may better explain the effects of soil sterilisation on mycelial differentiation and extension. It is difficult to be sure of the relative importance of each of these factors. However, interaction with other fungi has been shown to stimulate rhizomorph formation in *Sphaerostilbe repens* (Botton & El-Khouri, 1978) and cord formation in *P. velutina* (Rayner & Todd, 1979; see also Rayner & Webber: Chapter 18). Nevertheless *P. velutina* and *P.*

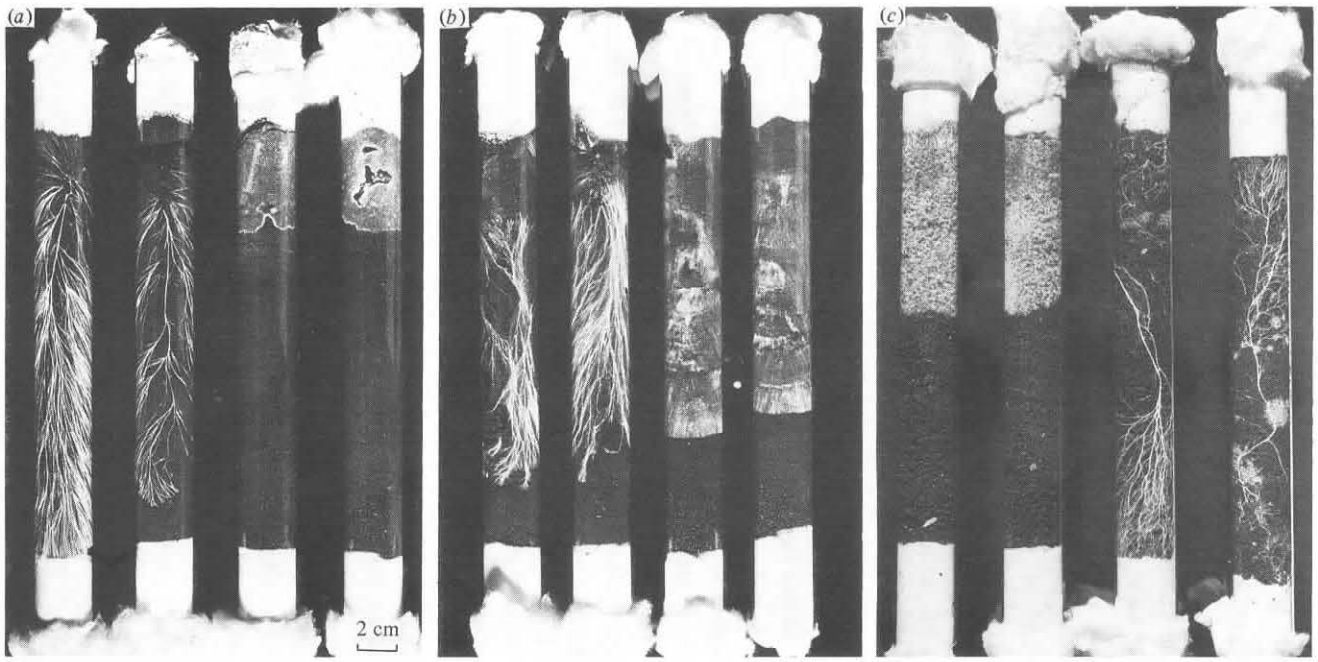

Fig. 6. Growth of cord-forming fungi in soil tubes. (a) *Steccherinum fimbriatum* and (b) *Hypholoma fasciculare* growing through non-sterile soil (left) and irradiated soil (right). (c) *Phanerochaete velutina* growing through irradiated soil (left) and non-sterile soil (right). (Thompson & Rayner, 1983.)

impudicus readily form cords when wood blocks colonised by these species are placed in wells in sterile Perspex cabinets, supplied with sterile distilled water and allowed to grow over Perspex platforms (Fig. 7). Clearly stimulation of cord formation by micro-organisms is most unlikely here and the absence of nutrients on the surface over which the mycelium is growing is the much more likely explanation.

Functioning

Colonisation of substrata

In the field. Detailed studies of the colonisation of various virgin substrata by cord-forming fungi (Thompson, 1982) have demonstrated the rapidity with which the latter can invade and colonise woody substrate. At one site colonisation of beech logs ($\sim 30 \times 10$ cm) by *P. velutina* (the most commonly found cord-forming species in this study) occurred within one month of the logs being laid on the woodland floor.

Large areas of the beech logs were initially colonised by *P. velutina* and other cord-forming fungi at those parts in contact with the litter and soil of the forest floor. The mycelia formed small cord systems which were closely associated with the tightly-packed leaf litter beneath the logs. From here cords spread onto and under the bark and over the cut ends of the logs. Genetical analysis of the mycelial types of *P. velutina* isolated throughout the experimental site indicated that a single individual/mycelial type was responsible for all colonisation by this species. This observation emphasises the effectiveness of vegetative propagation as a means of spread through soil and litter.

The speed with which cord-forming fungi invade newly supplied lignicolous substrata suggests that some stimulus may cause directed growth of cords towards the wood.

In the laboratory. The idea of substratum-directed growth to explain the rapid arrival of mycelia of cord-forming fungi at potential food bases has been further explored in the laboratory using an unidentified coprophilous cord-forming species. Autoclaved rabbit pellets, some colonised by the cord former and others left uncolonised, were arranged in glass Petri dishes containing sterile and non-sterile sand so that each pellet was equidistant from each of its neighbours. In sterile sand slow and limited mycelial growth usually occurred for a few millimetres around colonised pellets but no cords were observed. By contrast cord formation in non-sterile sand was extensive (Fig. 8) with the number of cords of diameter greater than 0.25 mm produced in each type of experimental

arrangement (i.e. a, b and c, Fig. 8) increasing with the number of pellets colonised originally. In experiments of type b most cords originating from the central colonised pellet grew directly towards those pellets which were originally uncolonised. Indeed in all cases where cord growth occurred this appeared to be directed towards particular pellets rather than at random. As with wood decay cord-forming fungi, growth

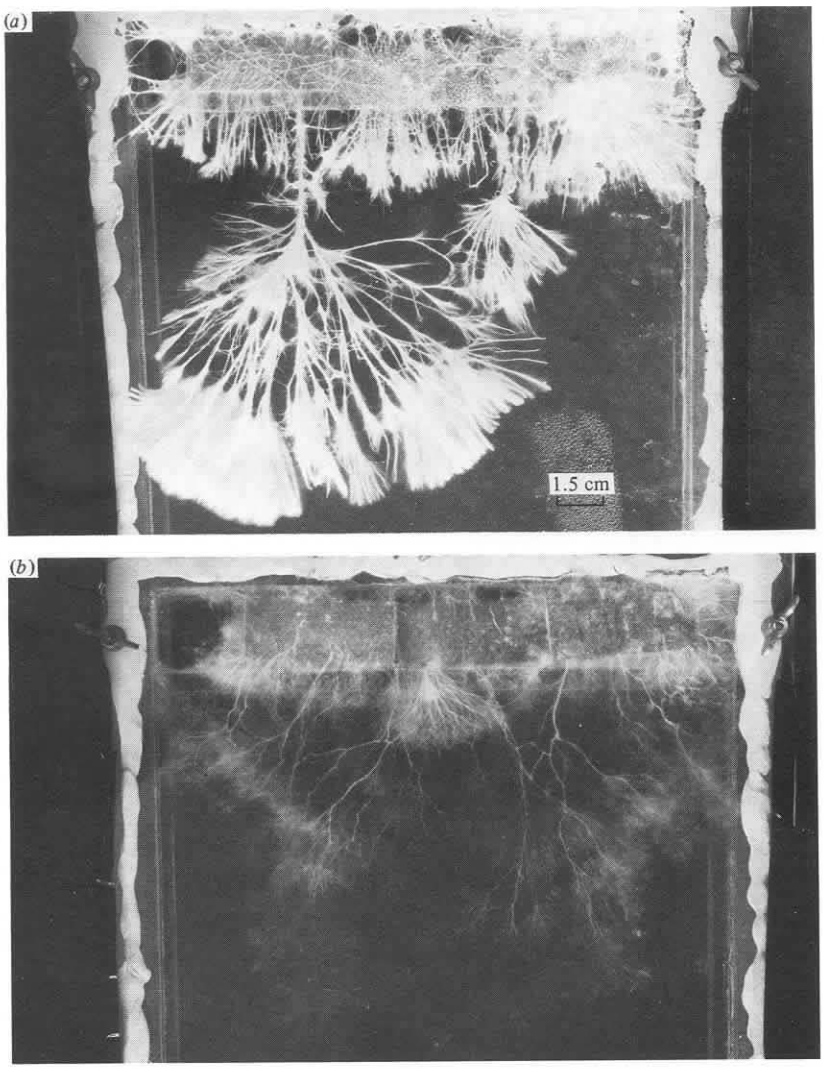

Fig. 7. (a) *Phallus impudicus* and (b) *Phanerochaete velutina* growing from colonised wood blocks over Perspex platforms in sterile chambers.

at the periphery of developing systems occurred as fans of fine cords which grew towards particular pellets and did not spread uniformly through the sand.

This apparently directional growth of cords may represent an efficient way in which a fungus can spread through the soil to potentially colonisable resources without energy being wasted on the multi-directional production of cords. These observations support the idea that certain stimuli, perhaps volatiles, may be important in stimulating and directing cord growth, in which case cord formation may be seen as an effective means of amplifying the sensitivity and responsiveness of individual hyphae and may explain why cord-forming fungi are attracted so rapidly to newly supplied potential food bases.

Resource utilisation and mobilisation

In the soil tube experiments described previously the weight losses of blocks colonised by *P. impudicus, P. velutina, P. laevis, S. fimbriatum* and *H. fasciculare* were significantly greater in irradiated soil than in non-sterile soil. Also when blocks colonised by *P. laevis* were analysed for nitrogen those from sterile soil were found to contain more nitrogen at the end of the experiment than at the beginning or than blocks from unsterilised soil. This extra nitrogen probably originated from the sterile soil and entered the blocks by direct diffusion or translocation by the mycelium. Thus higher nitrogen levels in sterile soil were associated with more decay and with the production of lesser amounts of mycelium, whilst in non-sterile soil lower nitrogen levels were associated with less decay and substantial cord growth. It would appear then that this species, and perhaps other cord-forming species, produced more extensive mycelial cord systems but cause less decay of wood at the food base in non-sterile soil, whilst in sterile soil, where nutrient levels are presumed to be higher, the fungus appears to be

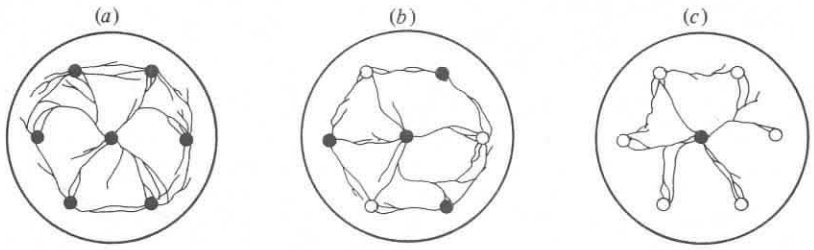

Fig. 8. Development of mycelial cords by a coprophilous basidiomycete in non-sterile sand. Filled circles, rabbit pellets colonised at start of experiment; hollow circles, pellets not colonised at start of experiment. (Thompson & Rayner, 1983.)

more confined to the food base and shows less tendency to explore the surrounding soil.

Interactions

Intraspecific: mycelial recognition phenomena. The existence of somatic incompatibility phenomena amongst cord-forming fungi has already been mentioned within the context of population structure. The occurrence of somatic acceptance and rejection phenomena between like and unlike genotypes respectively, raises the question as to how these might be mediated via aggregations of hyphae as opposed to diffuse mycelia where interactions between individual hyphae initiate the response. Observations of excavated field systems (see above) indicate that anastomoses between cords within the same system occur readily, sometimes over distances of the order of several centimetres. Laboratory studies with *P. velutina* have shown that mycelial cords of different individuals arising from wood-block inocula in non-sterile soil can grow towards one another and come into contact. In all cases when this happens fusions occur but while those between like mycelial types persist, those between different types are followed by discolouration and eventual death of the previously fused regions. This results in an 'avoidance reaction' and a lack of further growth into these areas (Fig. 9).

Interspecific: competition with Armillaria *species.* As has been indicated, colonisation of woody substrata by cord-forming fungi is often effected

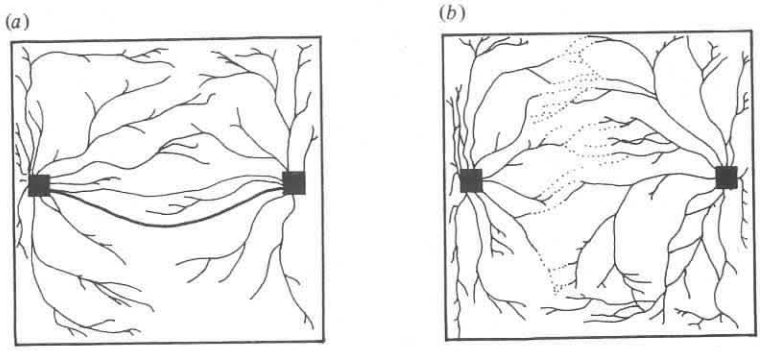

Fig. 9. Diagrammatic representation of (*a*) a compatible interaction between cord systems of the same mycelial type, and (*b*) an incompatible interaction between cord systems of different mycelial type of *Phanerochaete velutina* in non-sterile soil. Continuous lines, living mycelial cords; dotted lines, dead mycelial cords. (Thompson & Rayner, 1983.)

by extensive fans of mycelium, which are typically subcortical if bark is present. Production of the resulting sheath of mycelium allows considerable subsequent primary resource capture in competition with other fungi (see Rayner & Webber: Chapter 18) and hence occupation of large decay columns by one or a few individuals (see Rayner *et al.*: Chapter 23). This may have important practical implications in relation to competition with root pathogens, such as *Armillaria* species. The latter also have an ectotrophic habit and often produce abundant external mycelium and rhizomorphs, but this does not necessarily always imply that large volumes of wood are occupied (Rayner, 1975). In fact when *Armillaria* and cord-forming species occur together subcortically in dead wood the cord formers usually predominate in the actual decay, apparently having a competitive advantage over the former in purely saprotrophic situations (Rayner, 1975).

In the studies of suppressed trees mentioned previously, *A. bulbosa* was found only at one woodland site (the Forest of Dean) and *A. ostoyae* only at the other (Savernake). At Savernake forest 55% of sampled trees were colonised by cord-forming fungi, 42.5% by *A. ostoyae* and 27.5% by both cord-forming species and *A. ostoyae*. However at the Forest of Dean no trees were colonised by cord-forming fungi which were not also colonised by *A. bulbosa* (i.e. 69% were colonised by cord formers, 88% by *A. bulbosa* and 69% by both *A. bulbosa* and cord-forming fungi) (Table 3). These differences probably reflect the different ecological behaviour of the *Armillaria* species. *A. bulbosa* is a competitive saprotroph, although it can behave parasitically, and is far more common than was previously believed. Rishbeth (1982) clarified the distinctions between several *Armillaria* species and pointed out that *A. mellea sensu strictu*, which is highly pathogenic on both coniferous and deciduous trees, may not be as widespread as had previously been believed. Indeed in many cases *A. bulbosa*, which is a more prolific rhizomorph producer, has probably been misidentified as *A. mellea*. *A. ostoyae*, a rarer species which normally attacks conifers, is highly pathogenic and a less prolific rhizomorph producer.

These differences between *A. bulbosa* and *A. ostoyae* may explain why at Savernake certain suppressed individuals were colonised by cord formers but not *A. ostoyae*, as in the saprotrophic situation cord-forming fungi would have a competitive advantage over pathogens. At the Forest of Dean, *A. bulbosa* and cord-forming species share similar characteristics in that *A. bulbosa* can behave saprotrophically. Thus it might be expected that suppressed trees colonised by either a cord

former or an *Armillaria* species might also be colonised by the other, particularly as both cord formers and *A. bulbosa* are capable of producing extensive cord/rhizomorph networks in the soil.

Where cord-forming fungi and *Armillaria* species occurred together in the bases of suppressed trees, both occupied large volumes of wood. Usually, however, *Armillaria* was found in the lowest parts, whilst cord formers occupied greater volumes of wood at collar level. In most cases cord formers occupied peripheral regions, although they did sometimes spread considerable distances towards the central areas of roots (Fig. 10). The observation that cord-forming fungi occupied higher and peripheral regions whilst *Armillaria* species were limited to lower and more central regions may indicate that cord-forming fungi were actively replacing *Armillaria* species. Alternatively the *Armillaria* species may have invaded first (in lower regions) and come to occupy large volumes of wood, being restricted in higher regions by the cord-forming fungi which invaded later peripherally. This hypothesis that cord-forming fungi may limit or replace *Armillaria* species is supported by pairings in culture where all cord-forming species tested (*P. velutina, P. impudicus, T. platyphylla* and *H. fasciculare*) overgrew *A. bulbosa* and *A. ostoyae*. However, although in these pairings the latter were physically over-

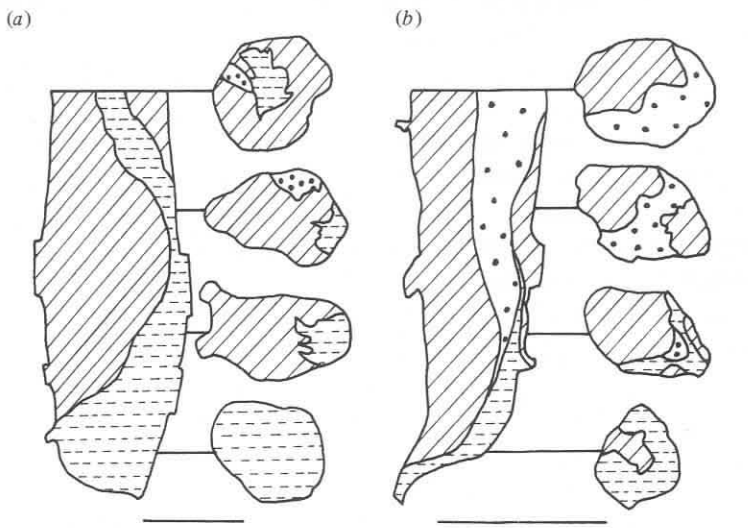

Fig. 10. Diagrammatic representation of the three-dimensional community structure of two representative roots from (a) Forest of Dean and (b) Savernake. Dashed areas, *Armillaria ostoyae* in (*a*), *A. bulbosa* in (*b*); hatched areas, *Phanerochaete velutina*; dotted areas, *Stereum hirsutum*. Scale bars, 10 cm. (Thompson & Boddy, 1983.)

grown they may not necessarily have been replaced. It is possible that the *Armillaria* species can seal themselves off from the overgrowing species, effectively retaining the potential for growth when suitable conditions arise. Also pairings of this type may not represent the situation which occurs in the woody tissues of a dead or dying tree (e.g. Rayner & Todd, 1979).

On the two main sites studied the dead trees had died at different times, some only in the year prior to study whilst others were in advanced stages of decay. The Savernake site consisted of the youngest trees, and in general the majority of dead trees there can be considered to have died fairly recently. This is borne out by the generally higher collar RDs of sampled trees from this site. (RD, relative density, is a means of estimating the state of decay of wood and is calculated as dry weight/volume. Living oak has an RD of 0.55–0.63 g cm^{-3} (Boddy & Thompson, 1983) and more decayed wood has lower RD values.) Fewer roots had been colonised by *A. ostoyae* or cord-forming fungi on this site than by *A. bulbosa* or cord-forming fungi in the Forest of Dean, and considerably fewer were colonised by the two types of fungi together at the former site. Also roots of trees from Savernake were generally at earlier stages of colonisation than at the Forest of Dean site. On both sites roots colonised by *A. bulbosa* or *A. ostoyae* tended to have higher RDs than those colonised by cord-forming fungi, possibly implying that the latter invade later than the former. Alternatively it may be that *A. bulbosa* and *A. ostoyae* decay wood less rapidly.

From a cursory study of an older oak stand (planted 1929) in the Forest of Dean, further hints as to processes of colonisation may be obtained. Of fifteen suppressed oak trees observed the roots of eight were colonised extensively, and almost exclusively, by *T. platyphylla*, one by *P. velutina*, two by *A. bulbosa* and one by both *T. platyphylla* and *A. bulbosa*. This may perhaps indicate that in older stands the saprotrophic cord-forming fungi were becoming increasingly dominant and had possibly replaced any *Armillaria* species in the roots of suppressed trees.

Cord-forming fungi may limit *Armillaria* species by occupying the same resource and thereby limiting the volume of wood (and amount of energy) available for *Armillaria* species for the production of rhizomorphs which may spread to neighbouring trees. Also by actively competing for the same resource cord-forming fungi may be more successful and outcompete the *Armillaria* at that time when no host resistance remains.

Using the technique of somatic incompatibility intra-specific pairings between different mycelial types of the two *Armillaria* species were made in addition to those between *P. velutina* isolates described earlier. The distribution of the two types of *A. ostoyae* found at Savernake and the two of *A. bulbosa* at the Forest of Dean are shown in Fig. 3. Isolates of the same mycelial type of *A. bulbosa* were found in suppressed trees 50 m apart, which again reflects the ability which fungi with a cord-forming/rhizomorphic habit have to spread in the forest floor.

Conclusions

This chapter has been concerned with the importance of mycelial cords in providing inter-communicating systems between spatially discontinuous woody resource units (food bases) on the forest floor, and their role in colonisation and vegetative spread. Understanding the dynamics of these systems provides a new challenge for mycologists, and the principles involved may differ substantially from those applying to diffuse mycelia on or in homogeneous media. Some features, such as branching patterns, formation of anastomoses, and somatic incompatibility, are reminiscent of phenomena exhibited by hyphae in diffuse mycelia but can be viewed on a macro- rather than a micro-scale.

Observations of the distribution of these fungi indicate the large dimensions their individual mycelia may achieve whilst also revealing the great extent to which populations of cord-forming fungi are distributed throughout the woodland floor. Cord-forming basidiomycetes then appear to be a ubiquitous group of saprotrophs in deciduous woodlands and play a major role as agents of decay of fallen wood and litter in forests. They may also be important, in certain situations, as natural and potential competitors against root-infecting fungi such as *Armillaria* species.

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